

DIVERSITY AND CONSERVATION OF BRYOPHYTES IN THE AMAZON-CERRADO TRANSITION OF NORTHEASTERN BRAZIL

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Recebido 06.07.2020; Aceito 15.10.2020

ABSTRACT

This checklist of the bryophyte species of the transitional Amazon-Cerrado in Northeastern Brazil characterizes the richness, provides the conservation assessment of the Brazilian-endemic taxa, their geographic distribution, and also presents new records for the Amazon Forest domain and the State of Maranhão. The checklist includes 101 species, 50 genera, and 22 families of bryophytes. The richest groups were Marchantiophyta (52 spp.), Lejeuneaceae (43 spp.), and the genera *Fissidens* and *Cheilolejeunea* (9 spp.). Three endemic Brazilian species had their conservation status assessed as Critically Endangered (CR). Two new records for the Amazon domain and 11 new records to the State of Maranhão were found. Our data demonstrate the potential of bryophyte floristic diversity in the regional (Amazon Forest from the State of Maranhão) and general (Amazon Forest domain) context, contributing to the knowledge of Neotropical bryophytes.

Keywords: Anthocerotophyta, Bryophyta, Liverworts, Marchantiophyta, Mosses.

RESUMO

Este catálogo das espécies de briófitas da transição Amazônia-Cerrado no Nordeste do Brasil caracteriza a riqueza, *status* de conservação dos táxons endêmicos do Brasil, distribuição geográfica e adição de novos registros para Floresta Amazônica e Estado do Maranhão. Foram catalogadas 101 espécies, 50 gêneros e 22 famílias de briófitas. Os grupos mais representativos foram Marchantiophyta (52 spp.), Lejeuneaceae (43 spp.) e os gêneros *Fissidens* e *Cheilolejeunea* (9 spp.). Três espécies endêmicas encontradas neste levantamento tiveram seus *status* de conservação avaliados como criticamente em perigo (CR). Foram encontrados dois novos registros para o domínio fitogeográfico da Amazônia e 11 novos registros para o Estado do Maranhão. Os dados apresentados são importantes para demonstrar o potencial da diversidade

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brioflorística no contexto regional (Floresta Amazônica do Estado do Maranhão) e geral (domínio Floresta Amazônica), contribuindo para o conhecimento da brioflora Neotropical.

Palavras-chave: Anthocerotophyta, Bryophyta, Hepáticas, Marchantiophyta, Musgos.

INTRODUCTION

The Amazon Forest covers approximately 5.4 million km² of nine countries in South America (Brazil, Peru, Colombia, Bolivia, Ecuador, Suriname, Venezuela, Guyana, and French Guiana), with its eastern limit in the State of Maranhão, Brazil. This region covers 24.46% of this State's area, with the lowest degree of occupation within conservation units. Furthermore, the Amazon forest in the State of Maranhão shows a high degree of deforestation and fragmentation, and one of the lowest rates of human development within eastern Amazon in Brazil. The region also encompasses the animal endemism center of Belém, the most threatened endemism center in the Amazon domain (Martins & Oliveira 2011).

The Amazon region is highly biodiverse, which contrasts with the reduced knowledge regarding its species and ecological relations, and their significantly unexplored economic potential (Ter Steege et al., 2016). However, there are still knowledge gaps regarding the richness and identity of plant species in this domain, which severely compromises the conservation actions for the region (Ter Steege et al., 2016), as well as the evolutionary and ecological processes that drive the local biodiversity (Souza et al., 2016; Baker et al., 2017). The diversity of plants in the Amazon is undersampled, in which the sample density equals ten collections per 100km². This generates the aforementioned knowledge gap related to the collection deficit, lack of taxonomists in certain botanical groups, and the unavailability of data (Sousa-Baena et al., 2014; Maldonado et al., 2015).

Maranhão is the only State in Northeastern Brazil, with near half of its area covered by the Amazon Forest (Muniz, 2011). This area is mostly represented by transition areas between the Amazon-Cerrado domains, featuring a myriad of ecosystems, ranging from mangroves, flooded grasslands to savannas (Muniz, 2011; Silva Junior et al., 2019). This ecotonal zone between the Cerrado and the Amazon domain in this State strongly influences the species' coverage and composition, as they need to adapt to the different abiotic conditions and tolerate weather changes (Martins & Oliveira, 2011). According to Martins (2011), the large extensions of Amazon-Cerrado ecotonal zones in the State of Maranhão have been considerably neglected by researchers. This lack of attention has helped to intensify the effect of changes in the local landscape, as well as in land use and agricultural expansion, for the past 50 years (Martins, 2011).

According to basic literature for the study of the species of bryophytes occurring in Brazil, are recognized essential guide of identification up until generic level carried out for Gradstein et al. (2001), the several Neotropics Flora (Reese, 1993; Pursell, 2007; Costa, 2008; Bischler-Causse et al., 2005) and guide of liverworts and hornworts of Gradstein & Costa (2003) and Worldwide Checklist of Söderström et al. (2016).

Brazil harbors about 1,574 species of mosses, hornworts, and liverworts, being the country with the richest bryoflora in the Neotropics (Costa & Peralta, 2015). Regarding the diversity of bryophytes in the Amazon, despite being an under-collected group of difficult identification, a total of 577 species are recognized in this biome (Costa & Peralta, 2020). The number of species of bryophytes has been increasing due to increased sampling efforts in hard-to-reach regions, which results in new distribution records. More recently, studies have reported new records for the Brazilian Amazon (Costa et al., 2017; Sierra et

aol., 2018, 2019; Garcia et al., 2020), as well as described new species (Brito & Ilkiu-Borges, 2012; Bastos & Zartman, 2016; Bastos et al., 2016).

Regarding the knowledge of bryophytes in Northeastern Brazil, we can highlight the studies of Yano & Andrade-Lima (1987), Pôrto (1990, 1992), Germano & Pôrto (1996, 1998), Valdevino et al. (2002), and Pôrto & Germano (2002) for the State of Pernambuco; Yano (1993) for the State of Paraíba; Yano (1994) for the State of Sergipe; Alvarenga et al. (2008, 2009, 2010), Oliveira et al. (2011), Silva & Pôrto (2009; 2010; 2013; 2015) for the State of Alagoas and Oliveira et al. (2019) for the State of Ceará. In a more extensive study, Yano et al. (2009) analyzed specimens from herbaria of several locations in the States of Ceará, Maranhão, Paraíba, Piauí, and Rio Grande do Norte, where they reported 143 taxa with 80 new distribution records. Knowledge about bryophytes in Northeastern Brazil focuses mainly on the Atlantic Rainforest domain. Many of these studies are from the States of Bahia, Pernambuco, and Alagoas, due to the larger number of bryologists in these or neighboring States (Silva & Pôrto, 2014). For the State of Maranhão, studies on bryophytes have increased significantly in the past ten years (e.g., Conceição et al., 2010; Santos & Conceição, 2010; Varão et al., 2011; Peralta et al., 2011; Macedo & Ilkiu-Borges, 2014; Brito & Ilkiu-Borges, 2014; Costa et al., 2015; Vieira et al., 2017; Oliveira et al., 2018a, b, c; Silva et al., 2018; Costa et al., 2018).

According to Costa & Peralta (2020), out of the 344 endemic bryophytes known to occur in Brazil, only 58 occur in the Amazon, while only five occur in the State of Maranhão (which never had their conservation status assessed). For many years, bryophytes were neglected in conservation programs, mainly due to the lack of knowledge on their distribution and ecology (Hallingbäck & Hodgetts, 2000). Assessing the conservation status of endemic taxa is essential to understand the threats affecting the bryoflora in major ecosystems such as the Amazon Forest, in addition to providing subsidies for conservation policies in the State and country (Costa & Santos, 2009).

However, there is a need to know the bryoflora of the Amazon region from the State of Maranhão, due to the ongoing loss of biodiversity caused by the advance of deforestation for extractivist activities, degradation of riparian forest, and bushfires, which significantly impact the knowledge of bryophytes in the eastern Amazon (Macedo & Ilkiu-Borges, 2014). Thus, our goal was to sample the bryophytes occurring in the Amazon-Cerrado transition of Northeastern Brazil (the Amazon region from the State of Maranhão). Furthermore, we aimed to contribute to a better understanding of this group by adding the data obtained from previously published studies for the region.

MATERIAL AND METHODS

Study area

The Amazon Forest region in the State of Maranhão, also known as eastern Amazon, is 81,208.40 km², representing 24.46% of the State of Maranhão (IBGE, 2002). Being a transition zone between the Amazon and Cerrado domains, the State of Maranhão presents conspicuous climatic and rainfall seasonalities. In the western region, the hot and humid tropical climate (As), typical of the Amazon region, predominates. In the remaining regions of the State, the climate is marked by a hot and semi-humid tropical climate (Aw). The vegetation cover of the State of Maranhão reflects, in particular, the influence of climatic transition conditions between the Amazonian climate and the Northeastern semi-arid (Martins, 2011; Santos et al., 2017). The region shows a humid climate, with little or no water deficiency, with seasonal restrictions regarding the

availability of water in its basins, where the soils are greatly varied (Costa et al., 2011; Santos et al., 2017).

Taxonomy

This study was based on herbaria/field studies and the review of published studies (Churchill, 1998; Brito & Ilkiu-Borges, 2014; Macedo & Ilkiu-Borges, 2014) for bryophytes from the Amazon Forest in the State of Maranhão. Field collections were carried out from June 2017 to July 2018 in the Quinto Braço community, municipality of Zé Doca (3° 16' 29" S and 45° 39' 29" W, Figure 1). The municipality is located in the Western Mesoregion of State of Maranhão, within the Microregion of Pindaré (IBGE, 2010). The collection, herborization, and preservation of the material followed Frahm (2003), consisting of random walks, for a thorough exploration of the study area. The specimens obtained in field studies were deposited in the bryological collection of the Laboratory of Plant Biology (LABIVE) from the Prof. Aluizio Bittencourt Herbarium (HABIT), Centro de Estudos Superiores de Caxias (CESC), State University of Maranhão (UEMA). Duplicates were sent to the Maria Eneyda Pacheco Kauffman Fidalgo Herbarium (SP) at the Instituto de Botânica de São Paulo.

For the registered species, several classification systems were consulted, since some groups of bryophytes underwent changes and updates in their taxonomy due to advances in phylogenetic systematics. However, for the three main bryophyte divisions, we adopted the classification systems based in Kruijer (2002), Crandall-Stotler et al. (2009), Frey & Stech (2009), Goffinet et al. (2009), Renzaglia et al. (2009), Costa et al. (2011), Gradstein (2015), Gradstein & Ilkiu-Borges (2015), Söderström et al. (2016), Carvalho-Silva et al. (2017) and Puttick et al. (2018).

Species identification was performed with the help of the studies by Florschütz (1964), Frahm (1991), Reese (1993), Lisboa (1993), Gradstein (1994), Ireland & Buck (1994), Sharp et al. (1994), Buck (1998), Buck (2003), Dauphin (2003), Gradstein & Costa (2003), Peralta (2005), Bordin & Yano (2013), Gradstein & Ilkiu-Borges (2009) and Reiner-Drehwald (2009). The scientific names of the species and authors presented were verified and updated through consultations on the digital platforms such as Flora do Brasil 2020 (Costa & Peralta 2020), Tropicos (2020), and International Plant Names Index (IPNI, 2020).

Conservation assessments

Information regarding geographic distribution, country endemism, and occurrence in phytogeographic domains were based on Costa & Peralta (2020), in addition to the following studies: Manuel (1977), Steere (1979), Pócs (1984), Schuster (1992), Gradstein & Costa (2003), Peralta (2005), Lai et al. (2008), Yano (2008), Costa (2010), Oliveira & Bastos (2010), Costa et al. (2011), Macedo & Ilkiu-Borges (2014), Oliveira & Bastos (2014), Peng & Zhu (2014), Costa & Peralta (2015), Sousa & Câmara (2015), Carmo et al. (2016), Carmo & Peralta (2016), Gupta et al. (2016), Costa et al. (2017), Carmo et al. (2018) and Amélio et al. (2019).

Conservation assessments for endemic species were performed according to Hallingbäck et al. (1996) and CNCFlora (2020). The list of cataloged species was organized in alphabetical order by division, family, genus, and species, with an indication of the source of registration, endemic species for Brazil, and new occurrences for the State of Maranhão and the Amazon Forest, having as reference Costa & Peralta (2020) and speciesLink (CRIA, 2020), besides the analysis of published studies for the State of Maranhão.

RESULTS AND DISCUSSION

We recorded 101 species of bryophytes, distributed in 50 genera and 22 families (Table 1) in the Amazon-Cerrado transition in the State of Maranhão, 17.5% of the species occurring in the Amazon Forest domain, according to Costa & Peralta (2020). These data could be higher, considering the various knowledge and sampling gaps within the Amazonian domain (Hopkins, 2007).

Table 1. List of bryophytes recorded in the Amazon-Cerrado transition in the State of Maranhão with the addition of new records. Geographical distribution worldwide (World distr.): Cosm = Cosmopolite; Ende = Endemic to Brazil; Neot = Neotropical; Pant = Pantropical; Phytogeographic domain (Phyt. dom.): Amazon Forest = AM, Atlantic Forest = AT, Cerrado = CE, Caatinga = CA, Pampa = PA, Pantanal = PN. Source: 1 - Brito & Ilkiu-Borges (2014); 2 – Macedo & Ilkiu-Borges (2014); 3 – Churchill (1998); 4 – Field collections from the present study. *: New records for the State of Maranhão; ♣: New record for the Amazon Forest; ♦ Species endemic to Brazil.

Taxa (Division/Family/Species)	World distr.	Phyt. dom.	Voucher
Anthocerotophyta			
Notothyladaceae			
<i>Notothylas orbicularis</i> (Schwein.) Sull. ⁴	Cosm	AM, CA, CE, MA	R.R. Oliveira 539 (HABIT)
Bryophyta			
Bartramiaceae			
<i>Philonotis uncinata</i> (Schwägr.) Brid. ⁴	Cosm	AM, CA, CE, MA, PA, PN	R.F. Oliveira 204 (HABIT)
Brachytheciaceae			
* <i>Zelometeorium ambiguum</i> (Hornsch.) Manuel ⁴	Pant	AM, MA	R.R. Oliveira 523 (HABIT)
** <i>Zelometeorium patens</i> (Hook.) Manuel ⁴		CE, MA	R.R. Oliveira 511 (HABIT)
Bryaceae			
** <i>Brachymenium acuminatum</i> Harv. ⁴	Cosm	CE, MA	R.R. Oliveira 515 (HABIT)
<i>Bryum apiculatum</i> Schwägr. ³	Cosm	AM, CA, CE, MA	Fróes 26772 (SP)
<i>Bryum coronatum</i> Schwägr. ³	Cosm	AM, CE, MA	Swallen 3628 (NY)
<i>Rosulabryum andicola</i> (Hook.) Ochyra ³	Pant	AM, CA, CE, MA, PA, PN	Schatz et al. 840-A (NY)
Calymperaceae			
<i>Calymperes erosum</i> Müll. Hal. ^{1,2}	Pant	AM, CE, MA	Bonadeu 537 (MG)
<i>Calymperes lonchophyllum</i> Schwägr. ^{1,2}	Pant	AM, CE, MA, PN	Macedo 859 (MG)
<i>Calymperes palisotii</i> Schwägr. ¹	Pant	AM, CA, CE, MT	R.F. Oliveira 195 (HABIT)

<i>Octoblepharum albidum</i> Hedw. ^{1,2}	Pant	AM, CA, CE, MA, PA, PN	Bonadeu 447 (MG)
<i>Syrrhopodon cymbifolius</i> Müll. Hal. ²	Neot	AM, CE, MA	Macedo 917; 921 (MG)
<i>Syrrhopodon gaudichaudii</i> Mont. ³	Pant	AM, CA, CE, MA, PN	Schatz et al. 840-B (NY)
<i>Syrrhopodon incompletus</i> Schwägr. ²	Pant	AM, CE, MA	Macedo 946; 949 (MG)
Fissidentaceae			
<i>Fissidens anguste-limbatus</i> Mitt. ⁴	Neot	AM, CA, CE, MA, PA, PN	R.R. Oliveira 124 (HABIT)
<i>Fissidens angustifolius</i> Sull. ²	Pant	AM, CA, CE, MA, PA, PN	Bonadeu 493; 496 (MG)
<i>Fissidens guianensis</i> Mont. ^{1,2}	Neot	AM, CA, CE, MA, PN	Bonadeu 502 (MG)
<i>Fissidens palmatus</i> Hedw. ²	Neot	AM, CE, MA	Macedo 704; 837 (MG)
<i>Fissidens pellucidus</i> Hornsch. ^{1,2}	Neot	AM, CA, CE, MA, PA, PN	Bonadeu 401; 460 (MG)
<i>Fissidens perfalcatus</i> Broth. ⁴	Neot	AM, CE, MA	R.R. Oliveira 131 (HABIT)
<i>Fissidens prionodes</i> Mont. ²	Neot	AM, CA, CE	Macedo 934; 965 (MG)
* <i>Fissidens ramicola</i> Broth. ⁴	Neot	AM, CE, MA	R.F. Oliveira 214 (HABIT)
<i>Fissidens zollingeri</i> Mont. ⁴	Pant	AM, CA, CE, MA, PN	R.F. Oliveira 85 (HABIT)
Leucobryaceae			
<i>Campylopus heterostachys</i> (Hampe) A. Jaeger ⁴	Neot	AM, CA, CE, MA	R.F. Oliveira 185 (HABIT)
Neckeraceae			
* <i>Isodrepanium lentulum</i> (Wilson) E. Britton ⁴	Neot	AM, CE, MA, PN	R.R. Oliveira 542 (HABIT)
* <i>Neckeropsis disticha</i> (Hedw.) Kindberg ⁴	Pant	AM, CE, MA, PN	R.R. Oliveira 529 (HABIT)
<i>Neckeropsis undulata</i> (Hedw.) Reichardt ⁴	Neot	AM, CA, CE, MA, PN	R.R. Oliveira 522 (HABIT)
Orthotrichaceae			
<i>Schlotheimia jamesonii</i> (Arnott) Mitt. ³	Neot	AM, CE, MA, PA	Santos et al. 722 (NY)
Pylaisiaceae			
<i>Chryso-hypnum diminutivum</i> (Hampe) W.R. Buck ⁴	Cosm	AM, CE, MA, PA, PN	R.R. Oliveira 540 (HABIT)
Pylaisiadelphaceae			
<i>Isopterygium subbrevisetum</i> (Hampe) Broth. ²	Neot	AM, MA	Bonadeu 443; 461 (MG)
<i>Isopterygium tenerifolium</i> Mitt. ⁴	Neot	AM, CE, MA	R.R. Oliveira 528 (HABIT)
<i>Isopterygium tenerum</i> (Sw.) Mitt. ¹	Cosm	AM, CA, CE, MA, PA, PN	R.R. Oliveira 532 (HABIT)
<i>Taxithelium planum</i> (Brid.) Britt. ^{1,2,3}	Neot	AM, CE, MA, PN	R.R. Oliveira 530 (HABIT)
* <i>Taxithelium pluripunctatum</i> (Renauld & Car-	Neot	AM, MA	R.F. Oliveira

dot) Broth. ⁴			208 (HABIT)
Pilotrichaceae			
<i>Callicostella pallida</i> (Hornsch.) Ångstr. ²	Neot	AM, CA, CE, MA, PA, PN	R.R. Oliveira 514 (HABIT)
<i>Lepidopilum scabrisetum</i> (Schwägr.) Steere ²	Neot	AM, CE, MA	Bonadeu 428 (MG)
Pterobryaceae			
<i>Henicodidium geniculatum</i> (Mitt.) W.R. Buck ⁴	Pant	AM, CE, MT, PN	R.F. Oliveira 183 (HABIT)
Sematophyllaceae			
<i>Brittonodoxa subpinnata</i> (Brid.) W.R. Buck, P.E.A.S. Câmara & Carv.-Silva ²	Pant	AM, CA, CE, MA, PA, PN	Macedo 1025 (MG)
* <i>Colobodontium vulpinum</i> (Mont.) S.P. Churchill & W.R. Buck ⁴	Neot	AM, CE, MA	R.R. Oliveira 543 (HABIT)
<i>Microcalpe subsimplex</i> (Hedw.) W.R. Buck ^{1,2,3}	Neot	AM, CA, CE, MA, PA, PN	R.F. Oliveira 179 (HABIT)
<i>Pterogonidium pulchellum</i> (Hook. f.) Müll. Hal. ex Broth. ⁴	Neot	AM, MA	R.F. Oliveira 210 (HABIT)
<i>Trichosteleum inundatum</i> (Mitt.) A. Jaeger ³	Neot	AM	Silva et al. 1097 (NY)
<i>Trichosteleum papillosum</i> (Hornsch.) A. Jaeger ^{1,2}	Neot	AM, CE, MA	Macedo 991; 996 (MG)
Stereophyllaceae			
<i>Entodontopsis leucostega</i> (Brid.) W.R. Buck & Ireland ³	Cosm	AM, CA, CE, MA, PN	Vilhena et al. 991 (NY)
<i>Pilosium chlorophyllum</i> (Hornsch.) Müll. Hal. ^{1,2}	Neot	AM, CE, MA PN	Macedo 1005; 1013 (MG)
Thuidiaceae			
<i>Pelekium involvens</i> (Hedw.) Touw ⁴	Cosm	AM, CE, MA, PN	R.F. Oliveira 15 (HABIT)
<i>Pelekium scabrosulum</i> (Mitt.) W.R. Buck & Crum ^{1,2}	Neot	AM, CE, MA	Bonadeu 423; 497 (MG)
<i>Pelekium schistocalyx</i> (Müll.Hal.) A. Touw ³	Neot	AM, CE, MA, PN	Daly et al. D503 (MO, NY);
Marchantiophyta			
Frullaniaceae			
<i>Frullania apiculata</i> (Reinw., Blume & Nees) Nees ²	Pant	AM, CE, MA	Macedo 985; 1025 (MG)
Lejeuneaceae			
<i>Acrolejeunea emergens</i> (Mitt.) Steph. ⁴	Pant	AM, CE, MA, PA, PN	R.R. Oliveira 533 (HABIT)
<i>Acrolejeunea torulosa</i> (Lehm. & Lindenb.) Schiffn. ⁴	Neot	AM, CE, MA, PN	R.R. Oliveira 512 (HABIT)
<i>Archilejeunea fuscescens</i> (Hampe ex Lehm.) Fulford ²	Neot	AM, MA	R.F. Oliveira 206 (HABIT)
<i>Caudalejeunea lehmanniana</i> (Gottsche) A. Evans ²	Pant	AM, CE, MA, PA	Bonadeu 623 (MG)
<i>Ceratolejeunea coarina</i> (Gottsche) Steph. ²	Neot	AM, CE, MA	Macedo 992;

<i>Ceratolejeunea cornuta</i> (Lindenb.) Schiffn. ²	Neot	AM, MA	1000 (MG) Macedo 1025 (MG)
<i>Ceratolejeunea guianensis</i> (Nees & Mont.) Steph. ²	Neot	AM, MA,	Macedo 873 (MG)
<i>Ceratolejeunea laetefusca</i> (Austin) R.M. Schust. ^{1,2}	Neot	AM, CE, MA	Macedo 724; 873 (MG)
* <i>Ceratolejeunea maranhensis</i> Silva Brito & Ilk.-Borg. ¹	Ende	AM	E.S. Brito 505 (MG)
<i>Ceratolejeunea minuta</i> Dauphin ²	Neot	AM, MA	Macedo 716; 996 (MG)
<i>Cheilolejeunea adnata</i> (Kunze) Grolle ^{1,2}	Neot	AM, CE, MA	Macedo 1002; 1003 (MG)
<i>Cheilolejeunea aneogyna</i> (Spruce) A. Evans ^{1,2}	Neot	AM, MA	Macedo 1025, 1027 (MG)
<i>Cheilolejeunea clausa</i> (Nees & Mont.) R.M. Schust. ⁴	Neot	AM, CE, MA, PN	R.F. Oliveira 184 (HABIT)
<i>Cheilolejeunea comans</i> (Spruce) R.M. Schust. ²	Neot	AM, MA	Bonadeu 630 (MG)
<i>Cheilolejeunea discoidea</i> (Lehm. & Lindenb.) Kachr. & R.M. Schust. ^{1,2}	Neot	AM, CE, MA, PN	Bonadeu 544; 616 (MG)
<i>Cheilolejeunea holostipa</i> (Spruce) Grolle & R.-L. Zhu ²	Neot	AM, MA	Bonadeu 519 (MG)
<i>Cheilolejeunea neblinensis</i> Ilkiu-Borges & Gradst. ^{1,2}	Neot	AM, MA	Macedo 985; 1009 (MG)
<i>Cheilolejeunea oncophylla</i> (Ångstr.) Grolle & Reiner ^{1,2}	Neot	AM, MA	Macedo 920; 899 (MG)
* <i>Cheilolejeunea urubuensis</i> (Zartmann & I.L. Ackerman) R.L. Zhu & Y.M. Wei. ^{1,2}	Ende	AM	Macedo 928 (MG)
<i>Cololejeunea camillii</i> (Lehm.) A. Evans ^{1,2}	Neot	AM, MA	Bonadeu 389; 616 (MG)
<i>Cololejeunea contractiloba</i> A. Evans ²	Neot	AM, MA	Bonadeu 618 (MG)
<i>Cololejeunea diaphana</i> A. Evans ^{1,2}	Pant	AM, CE, MA	Macedo 877; 898 (MG)
* <i>Cololejeunea microscopica</i> (Taylor) Schiffn ⁴	Pant	AM, MA	R.R. Oliveira 213 (HABIT)
<i>Dibrachiella auberiana</i> (Mont.) X.Q. Shi, R.L. Zhu & Gradst. ^{1,2}	Neot	AM, CE, MA	Macedo 873; 882 (MG)
<i>Dibrachiella parviflora</i> (Nees) X.Q. Shi, R.L. Zhu & Gradst. ^{1,2}	Neot	AM, MA	Macedo 968; 989 (MG)
<i>Diplasiolejeunea brunnea</i> Steph. ²	Neot	AM, CE, MA	Bonadeu 495 (MG)
<i>Harpalejeunea stricta</i> (Lindenb. & Gottsche) Steph. ^{1,2}	Neot	AM, MA	Macedo 905; 1020 (MG)
<i>Lejeunea adpressa</i> Nees ^{1,2}	Pant	AM, MA	Macedo 987; 993 (MG)
<i>Lejeunea boryana</i> Mont. ²	Neot	AM, MA	Macedo 993 (MG)
<i>Lejeunea caulicalyx</i> (Steph.) E. Reiner & Goda ^{1,2}	Neot	AM, CE, MA, PN	Macedo 856; 860 (MG)
<i>Lejeunea flava</i> (Sw.) Nees ⁴	Pant	AM, CA, CE, MA, PA, PN	R.F. Oliveira 101 (HABIT)
* <i>Lejeunea obidensis</i> Spruce ²	Ende	AM	Bonadeu 427; 538 (MG)
<i>Lejeunea obtusangula</i> Spruce ⁴	Neot	AM, MA	R.F. Oliveira 178 (HABIT)
<i>Lejeunea phyllobola</i> Nees & Mont. ^{1,2}	Neot	AM, CA, CE, MA, PN	Bonadeu 427 (MG)

<i>Lejeunea tapajosensis</i> Spruce ²	Neot	AM, MA	Bonadeu 424 (MG)
<i>Leptolejeunea elliptica</i> (Lehm. & Lindenb.) Schiffn. ^{1,2}	Neot	AM, CA, CE, MA	Macedo 877 (MG)
<i>Microlejeunea epiphylla</i> Bischl. ^{1,2}	Neot	AM, CA, CE, MA, PN	Macedo 902; 1010 (MG)
<i>Myriocoleopsis minutissima</i> (Sm) R.L.Zhu, Y.Yu & Pócs ⁴	Pant	AM, CA, CE, MA	R.F. Oliveira 175 (HABIT)
<i>Pictolejeunea picta</i> (Gottsche ex Steph.) Grolle ²	Neot	AM	Macedo 852; 978 (MG)
<i>Prionolejeunea denticulata</i> (F. Weber) Schiffn. ^{1,2}	Neot	AM, MA	Macedo 874; 995 (MG)
<i>Rectolejeunea emarginuliflora</i> (Gottsche) A. Evans ²	Neot	AM, MA	Macedo 1023 (MG)
<i>Rectolejeunea fragelliformis</i> A. Evans ²	Neot	AM, MA	Macedo 986; 1000 (MG)
<i>Stictolejeunea squamata</i> (Willd. ex Weber) Schiffn. ²	Neot	AM, CE, MA, PA	Macedo 992; 993 (MG)
Lophocoleaceae			
<i>Chiloscyphus liebmannianus</i> (Gottsche) J.J. Engel & R. M. Schust. ²	Neot	AM, CE, MA	Macedo 696; 866 (MG)
Plagiochilaceae			
* <i>Plagiochila disticha</i> (Lehm. & Lindenb.) Lindenb. ⁴	Neot	AM, CA, CE, MA, PN	R.F. Oliveira 190 (HABIT)
<i>Plagiochila montagnei</i> Nees ²	Neot	AM, MA	Macedo 885; 710 (MG)
* <i>Plagiochila patula</i> (Sw.) Lindenb. ⁴	Neot	AM, MA	R.R. Oliveira 517 (HABIT)
<i>Plagiochila rutilans</i> Lindenb. ²	Neot	AM, CE, MA	Macedo 893; 889 (MG)
Radulaceae			
<i>Radula flaccida</i> Lindenb. & Gottsche ex Steph. ²	Pant	AM, MA	Macedo 966; 997 (MG)
<i>Radula mammosa</i> Spruce ²	Neot	AM, MA	Macedo 862; 864 (MG)
Ricciaceae			
<i>Riccia vitalii</i> Jovet-Ast ⁴	Neot	AM, CA, CE, MA, PA, PN	R.R. Oliveira 120 (HABIT)

The Amazon contributed significantly to the diversification of bryophyte lineages, mainly due to the abiotic conditions that the rainforest provides, establishing an environment conducive to the spread within the closed, dense, and humid forest, offering all requirements for species colonization (Saldanha et al., 2018).

The data sampled categorized by division showed that Marchantiophyta (Liverworts) was the most representative group in the number of species (52 spp.), followed by the Bryophyta division (Mosses) with 48 species, and Anthocerotophyta was represented by a single species *Notothylas orbicularis* (Schwein.) Sull (Figure 2). Söderström et al. (2016) recognized 7,486 species accepted for liverworts and hornworts globally, demonstrating the diversity of the Marchantiophyta division across the globe, mainly by the representation of Lejeuneaceae, the most representative in the number of species in this study. The data presented corroborate those demonstrated by Geffert et al. (2013),

showing that several areas of temperate forests, boreal forests, and tundra demonstrated a considerable richness of bryophytes species. However, the Neotropical region represents the largest diversity of the group, mainly due to the presence of the Amazon Rainforest.

Considering the Marchantiophyta division and all families recorded in this study, Lejeuneaceae was the most representative in the number of species (43 spp.) and genera (17), evidencing a high diversity of species for the Amazon Forest in the State of Maranhão (Figure 3). Lejeuneaceae is the largest family among hardwood liverworts, with 71 genera and more than 1900 species distributed worldwide (Söderström et al., 2016). According to Gradstein (1995), the family is greatly diversified in tropical rainforests, mainly due to the availability of the living trunk substrate, through trees, shrubs, seedlings, and lianas, with high representativeness in all regions of Brazil.

Taking Bryophyta into account, Fissidentaceae (9 spp.) and Calymperaceae (7 spp.) were the most representative families in species number, and Sematophyllaceae the most representative in the number of genera (five) (Figure 4). Fissidentaceae is monophyletic (La Farge et al., 2000), and one of the largest families of mosses (Pursell et al., 1992), comprising a single genus, *Fissidens* Hedw., widely distributed worldwide, which inhabit a diversity of substrates in tropical forests (Lisboa, 1993; Gradstein et al., 2001).

For Sobreira (2018), Calymperaceae is very frequent and shows greater ecological amplitude than other families. Our study corroborates this study, with the species *Calymperes afzelii*, *C. erosum*, *C. lonchophyllum*, and *C. palisotii* occurring in several different ecosystems. These species are typical of anthropized areas due to their high tolerance to intense light, air pollution, and high temperatures (Lisboa & Ilkiu-Borges, 2001; Santos & Lisboa, 2003).

Regarding the most species-rich genera, *Fissidens* (9 spp.) and *Cheilolejeunea* (9 spp.) were the most representative (Figure 5). *Cheilolejeunea* presents 170 Pantropical species but is only represented by 46 species in Brazil (Söderström et al., 2016; Bastos, 2017). The members of this group were collected on tree bark, rock, and occasionally on soil, which supports colonization of various environments and greater diversification of lineages (Gradstein et al., 2001). *Fissidens* is a genus found on all continents, except in Antarctica, with the highest number of species in tropical regions, but diminishing towards the poles (Allen & Pursell, 2010). The genus occurs in all Brazilian biomes, mainly in more shaded vegetation and on soil, rocks, and tree trunks (Gradstein et al., 2001; Bordin, 2011).

Three endemic species from Brazil were recorded in the Amazon Forest of State of Maranhão (*Ceratolejeunea maranhensis*, *C. urubuensis*, and *Lejeunea obidensis*). When assessed for conservation status, it was found that all of them are critically endangered (CR), due to fall within at least three criteria assessment (i.e., geographic distribution, number of locations of occurrence, and population decline) proposed by Hallingbäck et al. (1996).

Regarding the endemic species, *C. maranhensis* shows a restricted distribution to the Amazon Forest from the State of Maranhão in a single square of 10 km², occurring in a single location, severely fragmented and in population decline, probably with less than 50 “mature individuals” (Brito & Ilkiu-Borges, 2012). *C. urubuensis* occurs only in the Amazon Forest in the States of Amazonas, Pará, and Maranhão, recorded in less than five (i.e., three) 10 km² areas and found only in three severely fragmented locations (a single location for each State), and in population decline, probably with less than 50 “mature individuals” (Zartman & Ackerman, 2002). *L. obidensis* occurs exclusively in the Amazon region, registered in the States of Pará and Maranhão, in less than five squares

of 10 km² (recorded in three) and found in three severely fragmented and population decline, probably also with less than 50 “mature individuals” (Spruce, 1884; Moura et al., 2013).

Due to uncontrolled deforestation and fragmentation, the State of Maranhão shows no forest core areas (outside protected areas) anymore. These forests no longer show the minimum size to ensure sustainable practices of forest management for timber production (Martins & Oliveira, 2011). In the Amazon Forest in the State of Maranhão, original forest cover diminished from 25% (24,700 km²) in 2016 to 24 % (23,967 km²) in 2019, and 6,038 km² of remaining forests were degraded by fires and/or illegal logging – processes related to high levels of violence against indigenous and rural communities, which damages the conservation of these three abovementioned endemic species (Silva Junior et al., 2020).

With the analysis of the distribution data of recorded species, we can observe an environmental significance, where not only endemic but all species that occur in the region are threatened. The Amazon Forest in the State of Maranhão has a strategic role in providing ecosystem services and conservation of biodiversity, including numerous endemic species threatened with extinction (Martins & Oliveira, 2011). Celentano et al. (2017) advise policymakers to urgently create protection mechanisms for primary and secondary forests and establish and implement a State restoration policy.

The conditions that contribute to the bryophyte endemism process are: the period by which the site was available for colonization; environmental diversity, especially moisture availability; and the isolation time of the population (Schofield, 1985). Exogenous factors, such as narrow ecological requirements, climate, and ecological constraints, limit reduced distribution, and local endemism (Frahm, 2008).

Five species are restricted to the Amazon Forest: *Ceratolejeunea maranhensis*, *Cheilolejeunea urubuensis*, *Lejeunea obidensis*, *Pictolejeunea picta*, and *Trichosteleum inundatum*. Our results add two additional species as new records for the Amazon Forest: *Brachymenium acuminatum* Harv., and *Zelometeorium patens* (Hook.) Manuel. Sierra et al. (2019), recognized 38 new records for the States of North Brazil and the country, demonstrating the potential that Amazon bryoflora has and how much still needs to be sampled. Bastos et al. (2016) suggest that there should be a continuous investment in research with bryophytes in the Brazilian Amazon, mainly due to the constant and numerous taxonomic and floristic novelties.

The present study adds 48 species to the Amazon bryoflora of Maranhão (Flora do Brasil 2020), which correspond to a 40% increase. This contributes to a better understanding of this group in the Amazon Forest in the State of Maranhão. Surveys focusing on bryophytes in the Brazilian Amazon represent a significant contribution to the knowledge of the diversity of the group in Brazil and the world with: new records for the country (Ellis et al., 2015, Costa, 2017, Costa et al., 2017, Oliveira-da-Silva & Ilkiu-Borges, 2018) and the descriptions of new species (Zartman & Ackerman, 2002, Moura et al., 2012, Brito & Ilkiu-Borges, 2012, Bastos & Zartman 2016, Bastos et al. 2016).

A total of 11 new records were found for the State of Maranhão, representing an increase of 14% in the species number (Costa & Peralta, 2020), although the data of bryophytes for Maranhão are outdated by the project Flora do Brasil 2020. According to Costa & Peralta (2020), 86 species are recorded for the State of Maranhão. However, Peralta et al. (2011) have already recognized a higher species number (i.e., 137 species) than that demonstrated in Flora do Brasil (2020). Over time several studies were published with new records for the State, such as Costa et al. (2015), Vieira et al. (2017), Costa et al. (2018), and Oliveira et al. (2018a, b, c, d). No real estimate of species

occurring in the State was ever carried out, making clear the need for a list of bryophytes for the State of Maranhão.

Aside from the species recorded here, 16 additional taxa were cited for the Amazon Forest in the State of Maranhão in the study of Brito & Ilkiu-Borges (2014), in which vouchers were not located in any of the visited Brazilian herbaria. Thus, those records were treated as dubious in our study but were cited in table 2, indicating their worldwide distribution and phytogeographic domain occurrence.

Table 2. List of bryophyte species mentioned, but not confirmed for the Amazon Forest in the State of Maranhão. Geographical distribution worldwide (World distr.); Phytogeographic domain (Phyt. dom.): Amazon Forest = AM, Atlantic Forest = AT, Cerrado = CE, Caatinga = CA, Pampa = PA, Pantanal = PN. (Neot = Neotropical; Pant = Pantropical).

Taxa (Division/Family/Species)	World distr.	Phyt. Dom.
Bryophyta		
Calymperaceae		
<i>Calymperes afzelii</i> Sw.	Pant	AM, CE, MA
<i>Syrrhopodon cryptocarpos</i> Dozy & Molk	Neot	AM, MA
<i>Syrrhopodon ligulatus</i> Mont.	Neot	AM, CE, MA
Fissidentaceae		
<i>Fissidens inaequalis</i> Mitt.	Neot	AM, CE, MA
Leucobryaceae		
<i>Campylopus surinamensis</i> Müll. Hal.	Neot	AM, CE, MA, PN
Sematophyllaceae		
<i>Trichosteleum subdemissum</i> (Besch.) A. Jaeger	Pant	AM, CE, MA
Marchantiophyta		
Frullaniaceae		
<i>Frullania gibbosa</i> Nees.	Neot	AM, CA, CE, MA, PN
Lejeuneaceae		
<i>Cheilolejeunea rigidula</i> (Nees ex Mont.) R.M. Schust.	Pant	AM, CA, CE, MA, PN
<i>Cololejeunea cardiocarpa</i> (Mont.) A. Evans	Pant	AM, CE, MA
<i>Cololejeunea sintenisii</i> (Steph.) Pócs	Neot	AM, MA
<i>Lejeunea laetevirens</i> Nees & Mont.	Neot	AM, CA, CE, MA, PN
<i>Microlejeunea bullata</i> (Taylor) Steph.	Neot	AM, CA, CE, MA, PA, PN
<i>Pycnolejeunea contigua</i> (Nees) Grolle	Pant	AM, MA
<i>Rectolejeunea versifolia</i> (Schiffn.) L.Söderstr. et A. Hagborg	Neot	AM, CE
<i>Thysananthus amazonicus</i> (Spruce) Schiffn.	Neot	AM, CE, MA
<i>Thysananthus auriculatus</i> (Wilson & Hook) Sukkharak & Gradst.	Pant	AM, MA

The data presented are essential to demonstrate the potential of the bryofloristic diversity of the Amazon Forest in the regional (within a single State) and general (Amazon Forest) contexts. This is currently especially relevant, where considerable changes in the composition of vegetation have been occurring due to climate change (Esquivel-Muelbert et al., 2018), and anthropization processes such as deforestation and fires (Ferrante & Fearnside, 2019). According to Lovejoy & Nobre (2018), the Amazon Forest is close to the deforestation limit that can be tolerated by regional ecosystems, threatening the region's biodiversity and native people, as well as the regional and global climate.

ACKNOWLEDGEMENTS

The authors would like to thank the State University of Maranhão/UEMA for the support offered during the development of this study, and the residents of Quinto Braço village for helping with logistics during fieldwork.

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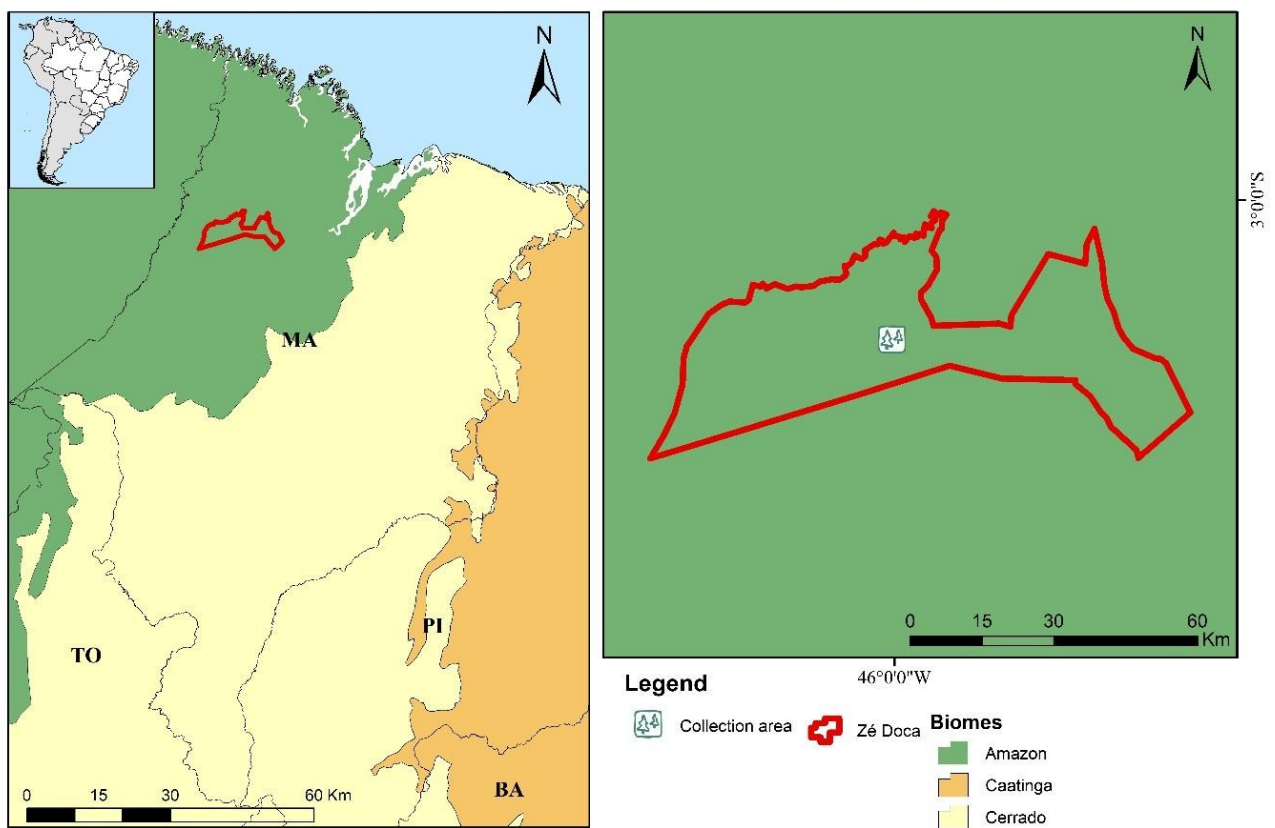


Figure 1. Location map of the study area within the Amazon Forest biome (Quinto Braço village, Municipality of Zé Doca, State of Maranhão, Brazil).

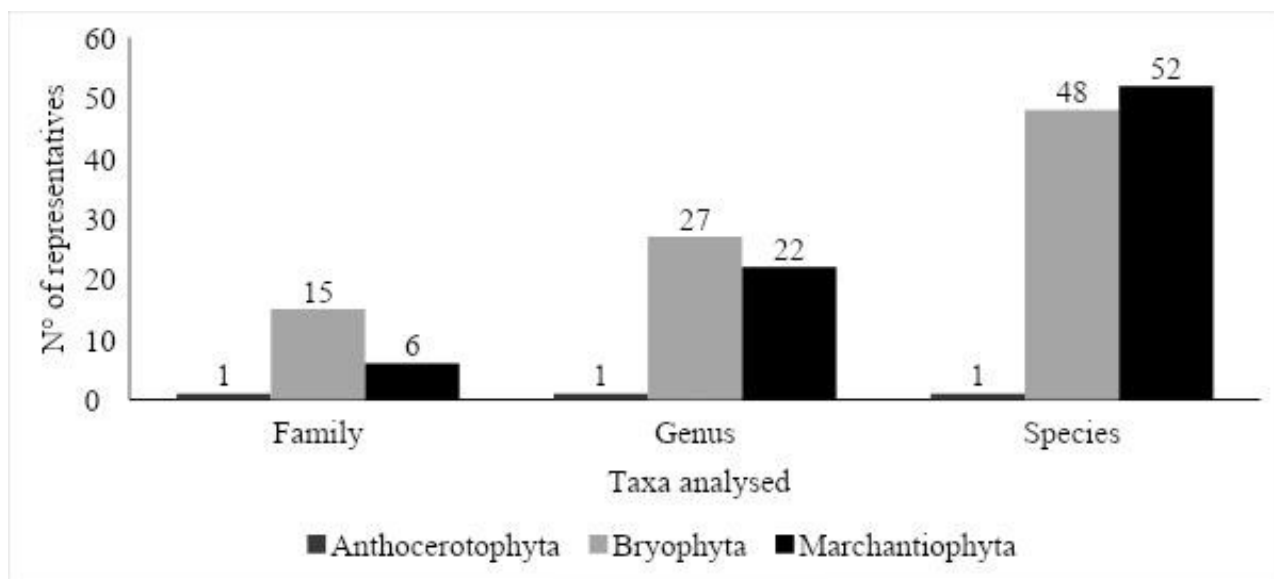


Figure 2. Distribution of the taxa (species, genera, and families) according to the division Marchantiophyta, Bryophyta and Anthocerotophyta recorded in the study area.

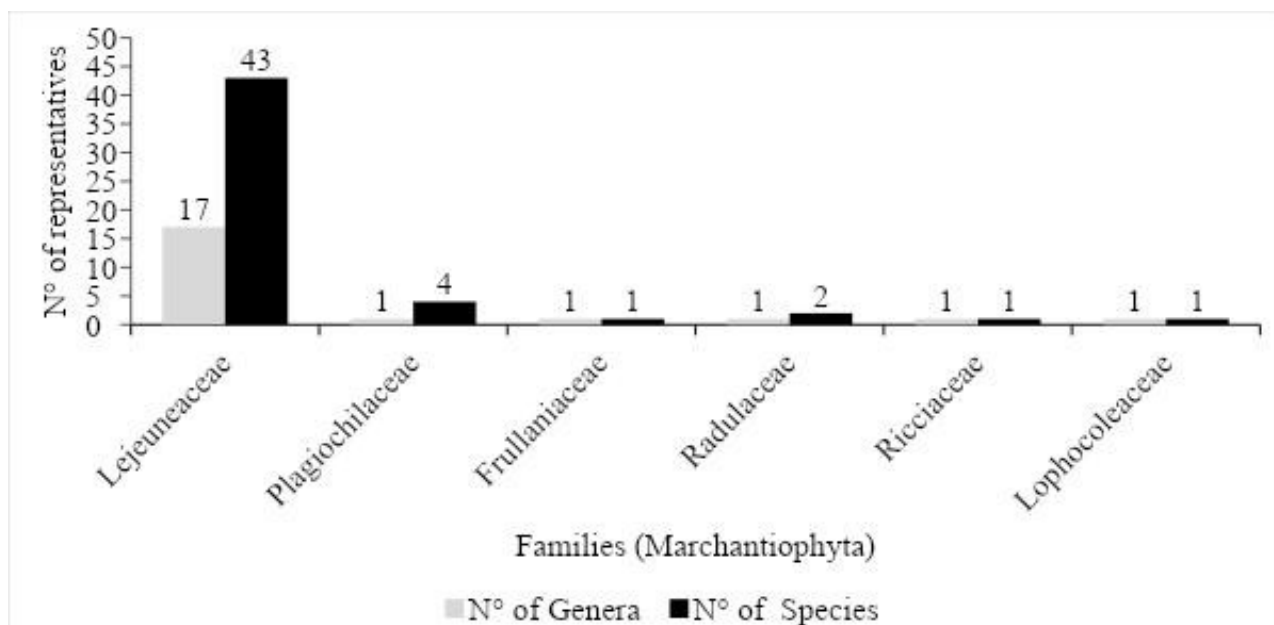


Figure 3. Distribution of the number of species and genera recorded per family of the Marchantiophyta division in the Amazon Forest in the State of Maranhão.

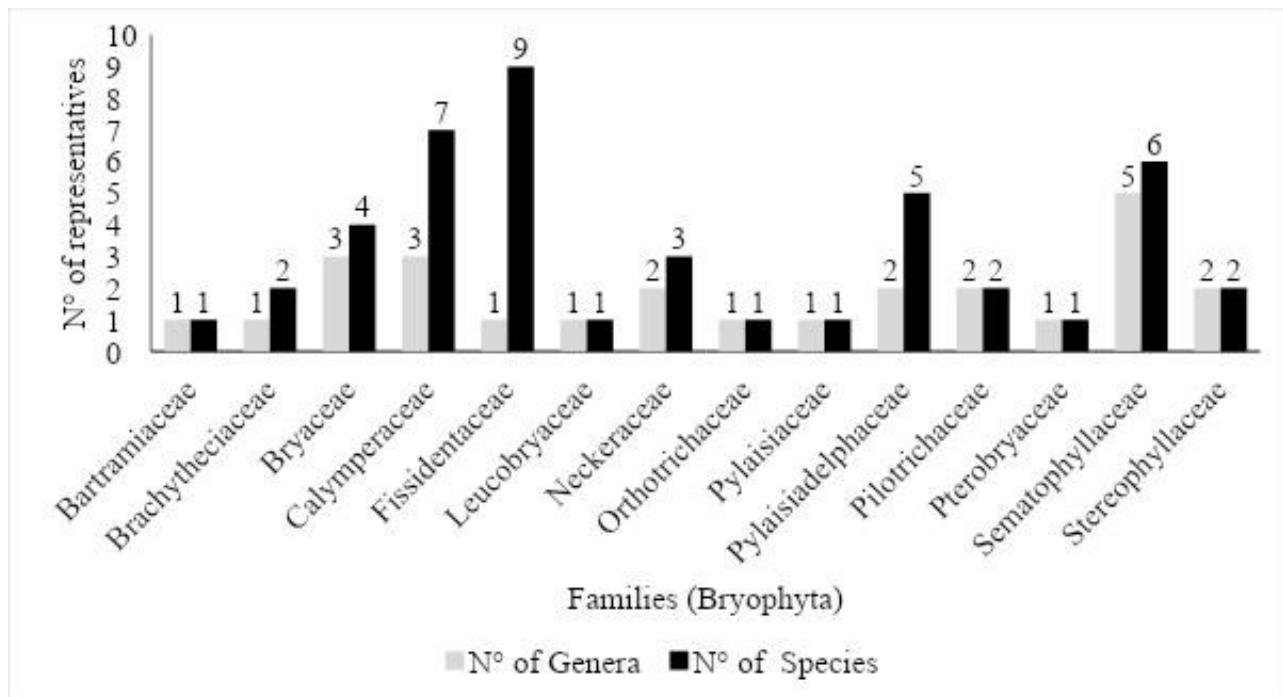


Figure 4. Distribution of the number of species and genera recorded per family of the Bryophyta division in the Amazon Forest in the State of Maranhão.

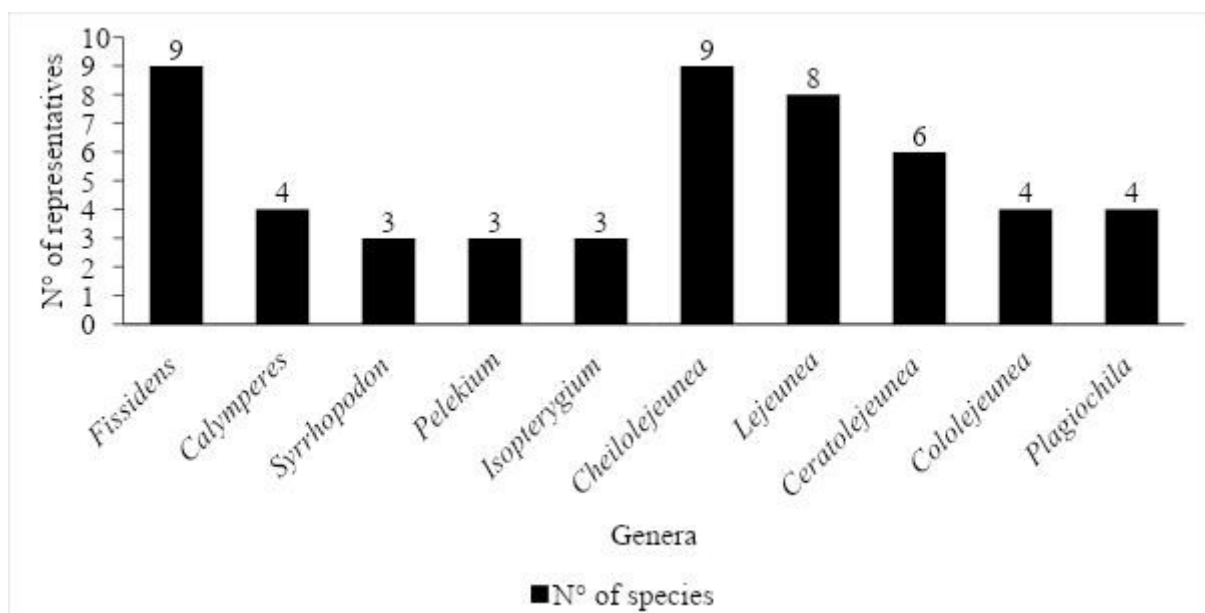


Figure 5. Distribution of the number of species per genus of each division (Bryophyta and Marchantiophyta) recorded in the Amazon Forest in the State of Maranhão.